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# Long-time behaviour of a stochastic prey–predator model☆

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**Abstract**

We consider a system of stochastic equations which models the population dynamics of a prey–predator type. We show that the distributions of the solutions of this system are absolutely continuous. We analyse long-time behaviour of densities of the distributions of the solutions. We prove that the densities can converge in $L^1$ to an invariant density or can converge weakly to a singular measure.
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## 1. Introduction

Consider the following system of stochastic equations:

$$\mathrm{d}X_t = \sigma X_t\,\mathrm{d}W_t + (\alpha X_t - \beta X_t Y_t - \mu X_t^2)\,\mathrm{d}t, \tag{1}$$

$$\mathrm{d}Y_t = \rho Y_t\,\mathrm{d}W_t + (-\gamma Y_t + \delta X_t Y_t - \nu Y_t^2)\,\mathrm{d}t, \tag{2}$$

where $\alpha$, $\beta$, $\gamma$, $\delta$, $\mu$, $\nu$, $\rho$ and $\sigma$ are positive constants. System (1), (2) is a stochastic version of a classical deterministic Lotka–Volterra prey–predator model

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(Volterra, 1931):

$$x' = x(\alpha - \beta y - \mu x), \qquad y' = y(-\gamma + \delta x - \nu y). \tag{3}$$

The stochastic processes $X_t$ and $Y_t$ represent, respectively, the prey and the predator populations and $\rho$, $\sigma$ are the coefficients of the effects of environmental stochastic perturbations on the prey and on the predator population. We assume here that the random noise for both populations is correlated, which corresponds to the situation when the same factor (like an epidemic disease) influences both prey and predator populations.

The existence, uniqueness and non-extinction property of the solution of this problem have been studied in Chessa and Fujita Yashima (2002). Substituting $X_t = e^{\xi_t}$ and $Y_t = e^{\eta_t}$ we replace system (1), (2) by

$$d\xi_t = \sigma \, dW_t + (\alpha - \sigma^2/2 - \mu e^{\xi_t} - \beta e^{\eta_t}) \, dt, \tag{4}$$

$$d\eta_t = \rho \, dW_t + (-\gamma - \rho^2/2 + \delta e^{\xi_t} - \nu e^{\eta_t}) \, dt. \tag{5}$$

The aim of this paper is to study the long-time behaviour of the solutions of system (4), (5). The asymptotic behaviour of system (4), (5) depends on the constants $\mu$, $\delta$, $c_1 = \alpha - \sigma^2/2$, and $c_2 = \gamma + \rho^2/2 > 0$. First, we show that the probability distributions of the process are absolutely continuous with respect to the Lebesgue measure. Let $u(x, y, t)$ be the density of the distribution of $(\xi_t, \eta_t)$. We give a sufficient and a necessary condition for asymptotic stability of system (4), (5), i.e. the convergence of $u(x, y, t)$ to a stationary density $u_*(x, y)$. In the case when this system is not asymptotically stable, we prove that $\lim_{t\to\infty} \xi_t = -\infty$ a.e. We also show that in this case $\lim_{t\to\infty} \eta_t = -\infty$ a.e. or the probability distributions of the process $\eta_t$ converge weakly to some probability measure.

The most difficult part of the paper is to show asymptotic stability of system (4), (5). This results from the fact that the Fokker–Planck equation corresponding to system (4), (5) is of a degenerate type. The strategy of the proof is the following. First, using the Hörmander condition (Norris, 1986) we show that the transition function of the process $(\xi_t, \eta_t)$ is absolutely continuous. Then using support theorems (Aida et al., 1993; Ben Arous and Léandre, 1991; Stroock and Varadhan, 1972) we find a set $E$ on which the density of the transition function is positive. Next, we show that the set $E$ is an "attractor". Then we apply results concerning asymptotic behaviour of partially integral Markov semigroups (Pichór and Rudnicki, 2000; Rudnicki, 1995). We show that the semigroup satisfies the "Foguel alternative", i.e. it is either asymptotically stable or "sweeping". Finally, we exclude sweeping by showing that there exists a Khasminskiĭ function. In this way we obtain asymptotic stability. In the case when this system is not asymptotically stable, we use stochastic inequalities to show that $\lim_{t\to\infty} \xi_t = -\infty$ a.e.

A similar technique was applied to study asymptotic behaviour of a large class of transport equations. The paper (Rudnicki et al., 2002) can be consulted for a survey of many results on this subject. It should be noted that the random perturbations of the Lotka–Volterra system were often considered in literature. Remarks concerning different random perturbations of (3) are given at the end of the paper. For example, it is much easier to study the Lotka–Volterra system with two-dimensional noise.

## 2. Asymptotic behaviour

In this section we formulate the main result of our paper. Let $(\xi_t, \eta_t)$ be a solution of (4), (5) such that the distribution of $(\xi_0, \eta_0)$ is absolutely continuous with the density $v(x, y)$. Then the random variable $(\xi_t, \eta_t)$ has the density $u(x, y, t)$ and $u$ satisfies the Fokker–Planck equation:

$$\frac{\partial u}{\partial t} = \frac{1}{2}\sigma^2\frac{\partial^2 u}{\partial x^2} + \sigma\rho\frac{\partial^2 u}{\partial x \partial y} + \frac{1}{2}\rho^2\frac{\partial^2 u}{\partial y^2} - \frac{\partial(f_1(x, y)u)}{\partial x} - \frac{\partial(f_2(x, y)u)}{\partial y}, \tag{6}$$

where $f_1(x, y) = c_1 - \mu e^x - \beta e^y$ and $f_2(x, y) = -c_2 + \delta e^x - \nu e^y$.

By $\mathscr{P}(t, x, y, A)$ we denote the transition probability function for the diffusion process $(\xi_t, \eta_t)$, i.e. $\mathscr{P}(t, x, y, A) = \text{Prob}((\xi_t, \eta_t) \in A)$ and $(\xi_t, \eta_t)$ is a solution of (4), (5) with the initial condition $(\xi_0, \eta_0) = (x, y)$.

Further we check that for each point $(x, y) \in \mathbb{R}^2$ and $t > 0$ the measure $\mathscr{P}(t, x, y, \cdot)$ is absolutely continuous with respect to the Lebesgue measure. Thus for $t > 0$ the distribution of any solution $(\xi_t, \eta_t)$ of (4), (5) is absolutely continuous with respect to the Lebesgue measure and its density $u$ satisfies (6).

**Theorem 1.** *Let $(\xi_t, \eta_t)$ be a solution of system* (4), (5). *Then for every $t > 0$ the distribution of $(\xi_t, \eta_t)$ has a density $u(t, x, y)$ which satisfies* (6).

(I) *If $c_1 > 0$ and $\mu c_2 < \delta c_1$ then there exists a unique density $u_*(x, y)$ which is a stationary solution of* (6) *and*

$$\lim_{t\to\infty} \iint_{\mathbb{R}^2} |u(x, y, t) - u_*(x, y)| \, dx \, dy = 0. \tag{7}$$

(II) *If $c_1 > 0$ and $\mu c_2 > \delta c_1$ then $\lim_{t\to\infty} \eta_t = -\infty$ a.e. and the distribution of the process $\xi_t$ converges weakly to the measure which has the density $f_*(x) = C\exp[2c_1 x/\sigma^2 - (2\mu/\sigma^2)e^x]$.*

(III) *If $c_1 < 0$ then $\lim_{t\to\infty} \xi_t = -\infty$ and $\lim_{t\to\infty} \eta_t = -\infty$ a.e.*

**Remark 1.** In case (I) the support of the invariant density $u_*$ depends on the coefficients $\rho$, $\sigma$, $\nu$, and $\beta$. If $\sigma > \rho$ or $\beta\rho \geqslant \nu\sigma$ then $u_* > 0$ a.e. If $\sigma \leqslant \rho$ and $\beta\rho < \nu\sigma$ then

$$\operatorname{supp} u_* = E(M_0) = \left\{(x, y):\ y < \left(\frac{\rho}{\sigma}\right)x + M_0\right\}, \tag{8}$$

where $M_0$ is the smallest number such that $f(x, y)\cdot[\rho, -\sigma] \geqslant 0$ for all $(x, y) \notin E(M_0)$, where $f = (f_1, f_2)$. By the *support* of a measurable function $f$ we simply mean the set

$$\operatorname{supp} f = \{(x, y) \in X:\ f(x, y) \neq 0\}.$$

This is not the customary definition of the support of a function, which is usually the closure of the set $\operatorname{supp} f$, but this slightly unusual definition is more suitable for our purposes.

**Remark 2.** Theorem 1 has an interesting biological interpretation. First observe that from (III) it follows that if $\alpha < \sigma^2/2$ then both prey and predator populations die out. If $c_1 = \alpha - \sigma^2/2 < 0$ then the prey population dies out even if there are no predators. In this case the process $X_t$ satisfies the equation

$$\mathrm{d}X_t = \sigma X_t \,\mathrm{d}W_t + (\alpha X_t - \mu X_t^2)\,\mathrm{d}t. \tag{9}$$

It is easy to check that

$$X_t \leqslant X_0 \exp(c_1 t + \sigma W_t)$$

and, consequently, $\lim_{t\to\infty} X_t = 0$. In the case without noise the prey population converges to a positive equilibrium. This means that a relatively large stochastic perturbation can cause the extinction of the population. We have a similar effect in the case $c_1 > 0$ and $\mu c_2 > \delta c_1$. Although the prey population converges to a stationary distribution, the predators die out because the diffusion coefficient $\rho$ is too large (and $c_2$ is too large). Of course, the prey population can also die out when the death coefficient $\gamma$ is too large or the prey population is too small (large $v$) or (small $\rho$), which takes place also in the case without noise. Therefore, the main difference between the deterministic and stochastic model is that large noise can also cause extinction. A completely unexpected situation is described in Remark 1 when $\operatorname{supp} u_* = E(M_0)$. Then the distribution of the system $(X_t, Y_t)$ can converge to a stationary distribution with some density $g_*$. Let a pair of variables $(X, Y)$ have the density distribution $g_*$. Then $Y \leqslant \mathrm{e}^{M_0} X^{\rho/\sigma}$. This means that the prey population precisely controls the number of predators.

## 3. Markov semigroups

We need some auxiliary results concerning Markov semigroups we will use later. Let the triple $(X, \Sigma, m)$ be a $\sigma$-finite measure space. Denote by $D$ the subset of the space $L^1 = L^1(X, \Sigma, m)$ which contains all densities, i.e.

$$D = \{f \in L^1\colon\ f \geqslant 0,\ \|f\| = 1\}.$$

A linear mapping $P : L^1 \to L^1$ is called a *Markov operator* if $P(D) \subset D$.

The Markov operator $P$ is called an *integral* or *kernel* operator if there exists a measurable function $k : X \times X \to [0, \infty)$ such that

$$Pf(x) = \int_X k(x, y) f(y) m(\mathrm{d}y) \tag{10}$$

for every density $f$. One can check that from the condition $P(D) \subset D$ it follows that

$$\int_X k(x, y)\, m(\mathrm{d}x) = 1 \tag{11}$$

for almost all $y \in X$.

A family $\{P(t)\}_{t\geqslant 0}$ of Markov operators which satisfies conditions:

(a) $P(0)=\mathrm{Id}$,
(b) $P(t+s)=P(t)P(s)$ for $s,t\geqslant 0$,
(c) for each $f\in L^1$ the function $t\mapsto P(t)f$ is continuous with respect to the $L^1$ norm

is called a *Markov semigroup*. A Markov semigroup $\{P(t)\}_{t\geqslant 0}$ is called integral, if for each $t>0$, the operator $P(t)$ is an integral Markov operator. That is, there exists a measurable function $k:(0,\infty)\times X\times X\to[0,\infty)$, called a *kernel*, such that

$$P(t)f(x)=\int_X k(t,x,y)f(y)\,m(\mathrm{d}y) \tag{12}$$

for every density $f$.

We need also two definitions concerning the asymptotic behaviour of a Markov semigroup. A density $f_*$ is called *invariant* if $P(t)f_*=f_*$ for each $t>0$. The Markov semigroup $\{P(t)\}_{t\geqslant 0}$ is called *asymptotically stable* if there is an invariant density $f_*$ such that

$$\lim_{t\to\infty}\|P(t)f-f_*\|=0 \quad \text{for } f\in D.$$

A Markov semigroup $\{P(t)\}_{t\geqslant 0}$ is called *sweeping* with respect to a set $A\in\Sigma$ if for every $f\in D$

$$\lim_{t\to\infty}\int_A P(t)f(x)\,m(\mathrm{d}x)=0. \tag{13}$$

**Remark 3.** The property of sweeping is also known as *zero type*. Some sufficient conditions for sweeping are given in Komorowski and Tyrcha (1989) and Rudnicki (1995). It is clear that if a Markov semigroup is sweeping from sets of finite measure then it has no invariant density. But even an integral Markov semigroup with a strictly positive kernel and having no invariant density can be non-sweeping from compact sets (see Rudnicki, 1995, Remark 7). Sweeping from compact sets is also not equivalent to sweeping from sets of finite measure (see Rudnicki, 1995, Remark 3). A semigroup can be both recurrent and sweeping, i.e. the heat equation $\partial u/\partial t=\Delta u$ generates a Markov semigroup on $L^1(\mathbb{R}^n)$ which is sweeping for all $n\geqslant 1$ but recurrent for $n=1,2$ and transient for $n\geqslant 3$. Also dissipativity does not imply sweeping (see Komorowski and Tyrcha, 1989, Example 1).

We need some results concerning asymptotic stability and sweeping which are based on the theory of Harris operators (Foguel, 1979).

**Theorem 2** (Pichór and Rudnicki, 2000). *Let $\{P(t)\}_{t\geqslant 0}$ be an integral Markov semigroup. Assume that the semigroup $\{P(t)\}_{t\geqslant 0}$ has only one invariant density $f_*$. If $f_*>0$ a.e. then the semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable.*

**Theorem 3** (Rudnicki, 1995). *Let $X$ be a metric space and let $\Sigma$ be the $\sigma$-algebra of Borel sets. We assume that an integral Markov semigroup $\{P(t)\}_{t\geqslant 0}$ has the following properties*:

(a) *for every $f\in D$ we have $\int_0^\infty P(t)f\,\mathrm{d}t>0$ a.e.*,
(b) *for every $y_0\in X$ there exist $\varepsilon>0$, $t>0$, and a measurable function $\eta\geqslant 0$ such that $\int \eta\,\mathrm{d}m>0$ and*

$$k(t,x,y)\geqslant \eta(x) \tag{14}$$

*for $x\in X$ and $y\in B(y_0,\varepsilon)$, where $B(y_0,\varepsilon)$ is the open ball with centre $y_0$ and radius $r$*,
(c) *the semigroup $\{P(t)\}_{t\geqslant 0}$ has no invariant density.*

*Then the semigroup $\{P(t)\}_{t\geqslant 0}$ is sweeping with respect to compact sets.*

From Theorems 2 and 3 the following corollary is immediate

**Corollary 1.** *Let $X$ be a metric space and let $\Sigma$ be the $\sigma$-algebra of Borel sets. Let $\{P(t)\}_{t\geqslant 0}$ be an integral Markov semigroup with a continuous kernel $k(t,x,y)$ for $t>0$, which satisfies (11) for all $y\in X$. We assume that for every $f\in D$ we have*

$$\int_0^\infty P(t)f\,\mathrm{d}t>0 \quad a.e. \tag{15}$$

*Then this semigroup is asymptotically stable or is sweeping with respect to compact sets.*

**Proof.** If the semigroup $\{P(t)\}_{t\geqslant 0}$ has an invariant density $f_*$ then from (15) it follows that $f_*>0$ a.e. If a Markov semigroup has two different invariant densities then it has two invariant densities with disjoint supports, which is impossible in our case. Thus the semigroup $\{P(t)\}_{t\geqslant 0}$ has at most one invariant density. Fix $t>0$ and $y_0\in X$. Since $\int_X k(t,x,y_0)m(\mathrm{d}x)=1$ there exist an $x_0\in X$ and a $\lambda>0$ such that $k(t,x_0,y_0)>\lambda$. From continuity of the kernel $k$ it follows that there exists an $\varepsilon>0$ such that $k(t,x,y)>\lambda$ for $x\in B(x_0,\varepsilon)$ and $y\in B(y_0,\varepsilon)$. Let $\eta(x)=\lambda\mathbf{1}_{B(x_0,\varepsilon)}(x)$. Then $k(t,x,y)\geqslant\eta(x)$ for $x\in X$ and $y\in B(y_0,\varepsilon)$ and condition (14) holds. $\square$

The property that a Markov semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable or sweeping from a sufficiently large family of sets (e.g. from all compact sets) is called the *Foguel alternative* (Lasota and Mackey, 1994).

Now we introduce a Markov semigroup connected with the Fokker–Planck equation (6). Let $X=\mathbb{R}^2$, $\Sigma$ the $\sigma$-algebra of Borel subsets of $X$, and $m$ the Lebesgue measure on $(X,\Sigma)$. Let $P(t)v(x,y)=u(x,y,t)$ for $v\in D$. Since the operator $P(t)$ is a contraction on $D$, it can be extended to a contraction on $L^1(\mathbb{R}^2,\Sigma,m)$. Thus the operators $\{P(t)\}_{t\geqslant 0}$ form a Markov semigroup. Let $\mathscr{A}$ be the infinitesimal generator of the semigroup

$\{P(t)\}_{t\geqslant 0}$, i.e.

$$\mathscr{A}v = \frac{1}{2}\sigma^2\frac{\partial^2 v}{\partial x^2} + \sigma\rho\frac{\partial^2 v}{\partial x\partial y} + \frac{1}{2}\rho^2\frac{\partial^2 v}{\partial y^2} - \frac{\partial(f_1 v)}{\partial x} - \frac{\partial(f_2 v)}{\partial y}. \tag{16}$$

The adjoint operator of $\mathscr{A}$ is of the form

$$\mathscr{A}^* v = \frac{1}{2}\sigma^2\frac{\partial^2 v}{\partial x^2} + \sigma\rho\frac{\partial^2 v}{\partial x\partial y} + \frac{1}{2}\rho^2\frac{\partial^2 v}{\partial y^2} + f_1\frac{\partial v}{\partial x} + f_2\frac{\partial v}{\partial y}. \tag{17}$$

In Lemma 1 we prove that for each point $(x_0, y_0)\in\mathbb{R}^2$ and $t>0$ the measure $\mathscr{P}(t,x_0,y_0,\cdot)$ is absolutely continuous with respect to the Lebesgue measure. Denote by $k(t,x,y;x_0,y_0)$ the density of $\mathscr{P}(t,x_0,y_0,\cdot)$. Then

$$P(t)v(x,y) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} k(t,x,y;\xi,\eta)v(\xi,\eta)\,\mathrm{d}\xi\,\mathrm{d}\eta \tag{18}$$

and consequently $\{P(t)\}_{t\geqslant 0}$ is an integral Markov semigroup. Each solution $(\xi_t,\eta_t)$ of (4), (5) has for $t>0$ a density $u(x,y,t)$ and the function $u$ satisfies (6). Thus asymptotic stability of the semigroup $\{P(t)\}_{t\geqslant 0}$ implies the convergence in $L^1$ of the densities of the process $(\xi_t,\eta_t)$ to the invariant density. Therefore instead of proving part (I) of Theorem 1 we show asymptotic stability of the semigroup $\{P(t)\}_{t\geqslant 0}$.

## 4. Proofs

We divide the proof of Theorem 1 into lemmas.

**Lemma 1.** *$\{P(t)\}_{t\geqslant 0}$ is an integral Markov semigroup with a continuous kernel $k$.*

**Proof.** In the proof of this lemma we use the Hörmander theorem on the existence of smooth densities of the transition probability function for degenerate diffusion processes. A probabilistic proof of this result was made by Malliavin (1978a, b) and now it is a part of Malliavin calculus. We recall some results from this theory. If $a(x)$ and $b(x)$ are vector fields on $\mathbb{R}^d$ then the Lie bracket $[a,b]$ is a vector field given by

$$[a,b]_j(x) = \sum_{k=1}^{d}\left(a_k\frac{\partial b_j}{\partial x_k}(x) - b_k\frac{\partial a_j}{\partial x_k}(x)\right).$$

Let $a_0(\xi,\eta) = (c_1 - \mu\mathrm{e}^{\xi} - \beta\mathrm{e}^{\eta}, -c_2 + \delta\mathrm{e}^{\xi} - \nu\mathrm{e}^{\eta})$ and $a_1 = (\sigma,\rho)$. Then

$$[a_0,a_1](\xi,\eta) = (\sigma\mu\mathrm{e}^{\xi} + \rho\beta\mathrm{e}^{\eta}, -\sigma\delta\mathrm{e}^{\xi} + \rho\nu\mathrm{e}^{\eta}),$$

$$[a_1,[a_0,a_1]](\xi,\eta) = (\sigma^2\mu\mathrm{e}^{\xi} + \rho^2\beta\mathrm{e}^{\eta}, -\sigma^2\delta\mathrm{e}^{\xi} + \rho^2\nu\mathrm{e}^{\eta}).$$

If $\sigma\neq\rho$ then at any point $(\xi,\eta)$ vectors $a_1$, $[a_0,a_1]$, and $[a_1,[a_0,a_1]]$ span $\mathbb{R}^2$. If $\sigma=\rho$ then

$$[a_0,[a_0,a_1]](\xi,\eta) = \sigma(c_1\mu\mathrm{e}^{\xi} - c_2\beta\mathrm{e}^{\eta}, -c_1\delta\mathrm{e}^{\xi} - c_2\nu\mathrm{e}^{\eta})$$

and $c_1 + c_2 = \alpha + \gamma > 0$. This implies that at any point $(\xi, \eta)$ vectors $a_1$, $[a_0, a_1]$, $[a_0, [a_0, a_1]]$ span $\mathbb{R}^2$. Thus the vector fields $a_0$ and $a_1$ satisfy the Hörmander condition:

(H) For every $(\xi, \eta) \in \mathbb{R}^2$ vectors

$$a_1(\xi, \eta), [a_i, a_j](\xi, \eta)_{0 \leqslant i,j \leqslant 1}, \quad [a_i, [a_j, a_k]](\xi, \eta)_{0 \leqslant i,j,k \leqslant 1}, \ldots$$

span the space $\mathbb{R}^2$.

Under hypothesis (H) the transition probability function $\mathscr{P}(t, x_0, y_0, A)$ has a density $k(t, x, y; x_0, y_0)$ and $k \in C^\infty((0, \infty) \times \mathbb{R}^2 \times \mathbb{R}^2)$ (see Norris, 1986). □

Now we briefly describe the method based on support theorems (Aida et al., 1993; Ben Arous and Léandre, 1991; Stroock and Varadhan, 1972) which allows us to check where the kernel $k$ is positive. Fix a point $(x_0, y_0) \in \mathbb{R}^2$ and a function $\phi \in L^2([0, T]; \mathbb{R})$. Consider the following system of integral equations:

$$x_\phi(t) = x_0 + \int_0^t (\sigma\phi(s) + f_1(x_\phi(s), y_\phi(s)))\,\mathrm{d}s, \tag{19}$$

$$y_\phi(t) = y_0 + \int_0^t (\rho\phi(s) + f_2(x_\phi(s), y_\phi(s)))\,\mathrm{d}s. \tag{20}$$

Let $D_{x_0, y_0; \phi}$ be the Frechét derivative of the function $h \mapsto x_{\phi+h}(T)$ from $L^2([0, T]; \mathbb{R})$ to $\mathbb{R}^2$. If for some $\phi \in L^2([0, T]; \mathbb{R})$ the derivative $D_{x_0, y_0; \phi}$ has rank 2 then $k(T, x, y; x_0, y_0) > 0$ for $x = x_\phi(T)$ and $y = y_\phi(T)$. The derivative $D_{x_0, y_0; \phi}$ can be found by means of the perturbation method for ordinary differential equations. Namely, let $\Lambda(t) = f'(x_\phi(t), y_\phi(t))$ and let $Q(t, t_0)$, for $T \geqslant t \geqslant t_0 \geqslant 0$, be a matrix function such that $Q(t_0, t_0) = I$, $\partial Q(t, t_0)/\partial t = \Lambda(t) Q(t, t_0)$, and $\mathbf{v} = [{\sigma \atop \rho}]$. Then

$$D_{x_0, y_0; \phi} h = \int_0^T Q(T, s)\mathbf{v}h(s)\,\mathrm{d}s. \tag{21}$$

**Lemma 2.** *Let $E = \mathbb{R}^2$ when $\sigma > \rho$ or $\beta\rho \geqslant \nu\sigma$, and $E = E(M_0)$ when $\sigma \leqslant \rho$ and $\beta\rho < \nu\sigma$. Then for each $(x_0, y_0) \in E$ and for almost every $(x, y) \in E$ there exists $T > 0$ such that $k(T, x, y; x_0, y_0) > 0$.*

**Proof.** Since we only consider a continuous control function $\phi$, the system (19), (20) can be replaced by the following system of differential equations:

$$x'_\phi = \sigma\phi + c_1 - \mu \mathrm{e}^{x_\phi} - \beta \mathrm{e}^{y_\phi}, \tag{22}$$

$$y'_\phi = \rho\phi - c_2 + \delta \mathrm{e}^{x_\phi} - \nu \mathrm{e}^{y_\phi}. \tag{23}$$

*Step* 1: First, we check that there is a constant $C$ such that the rank of $D_{x_0, y_0; \phi}$ is 2 if $y \neq x + C$, where $x = x_\phi(T)$ and $y = y_\phi(T)$. Let $\varepsilon \in (0, T)$ and $h = \mathbf{1}_{[T-\varepsilon, T]}$.

Since $Q(T,s) = I - \Lambda(T)(T-s) + o(T-s)$, from (21) we obtain

$$D_{x_0,y_0;\phi} h = \varepsilon \mathbf{v} - \tfrac{1}{2}\varepsilon^2 \Lambda(T)\mathbf{v} + o(\varepsilon^2). \tag{24}$$

Since $\mathbf{v} = [\sigma, \rho]$ and $\Lambda(T)\mathbf{v} = e^x[-\mu\sigma - \beta\rho e^{y-x}, \delta\sigma - \nu\rho e^{y-x}]$, there is a constant $C$ such that these vectors are linearly independent if $y - x \neq C$. Thus $D_{x_0,y_0;\phi}$ has rank 2.

*Step* 2: Let $z_\phi(t) = y_\phi(t) - \sigma^{-1}\rho x_\phi(t)$ then system (22), (23) can be replaced by

$$x'_\phi = \sigma\phi + g_1(x_\phi, z_\phi), \tag{25}$$

$$z'_\phi = g_2(x_\phi, z_\phi), \tag{26}$$

where

$$g_1(x,z) = c_1 - \mu e^x - \beta e^{rx} e^z \quad \text{and} \quad g_2(x,z) = a_1 e^x + a_2 e^{rx} e^z - a_3, \tag{27}$$

$a_1 = \delta + \sigma^{-1}\rho\mu > 0$, $a_2 = \sigma^{-1}\rho\beta - \nu$, $a_3 = \sigma^{-1}\rho c_1 + c_2 > 0$, and $r = \sigma^{-1}\rho$. Fix $z_0, z_1 \in \mathbb{R}$ and $z_1 < z_0$. Then there exists $x_0 \in \mathbb{R}$ such that

$$g_2(x_0, z) \leqslant -a_3/2 \tag{28}$$

for $z \in [z_1, z_0]$. Consider system (25), (26) with $x_\phi \equiv x_0$ and $z_\phi(0) = z_0$. From (26), (28) it follows that there exist functions $\phi$, $z_\phi$ satisfying system (25), (26) and $z'_\phi \leqslant -a_3/2$. Consequently, we find $\phi$ and $T > 0$ such that $z_\phi(T) = z_1$.

*Step* 3: Now we assume that $r \in (0,1)$ or $a_2 \geqslant 0$. Then for every $z_0, z_1 \in \mathbb{R}$ and $z_0 < z_1$ there exists $x_0 \in \mathbb{R}$ such that $g_2(x_0, z) \geqslant 1$ for $z \in [z_1, z_0]$. Then we find a control function $\phi$ such that $x_\phi \equiv x_0$, $z_\phi(0) = z_0$ and $z_\phi(T) = z_1$ for some $T > 0$.

*Step* 4: Consider the case $r \geqslant 1$ and $a_2 < 0$. Then for every $\varepsilon > 0$ there exists a $\delta > 0$ having the following property. If $z_1 - \delta \leqslant z_0 < z_1 \leqslant M_0 - \varepsilon$ then there exists $x_0$ such that $g_2(x_0, z) \geqslant \delta$ for $z \in [z_0, z_1]$. Then we also find a control function $\phi$ such that $x_\phi \equiv x_0$, $z_\phi(0) = z_0$ and $z_\phi(T) = z_1$ for some $T > 0$.

*Step* 5: Fix $x_0 \in \mathbb{R}$, $L > 0$, $A_0$, $A_1 > A_0$ and $\varepsilon > 0$ such that $\varepsilon < L/4$ and $\varepsilon < (A_1 - A_0)/4$. Let

$$m = \max\{|g_1(x,z)| + |g_2(x,z)|\colon x \in [x_0, x_0 + L],\ z \in [A_0, A_1]\},$$

and $t_0 = \varepsilon m^{-1}$, $\phi \equiv 3\sigma^{-1}\varepsilon^{-1} mL/4$. Then for every $z_0 \in [A_0 + \varepsilon, A_1 - \varepsilon]$ the solution of system (25), (26) with $x_\phi(0) = x_0$ and $z_\phi(0) = z_0$ has the following properties:

$$z_\phi(t) \in [z_0 - \varepsilon, z_0 + \varepsilon] \quad \text{for } t \leqslant t_0 \quad \text{and} \quad x_\phi(t_0) \in (x_0 + L/2, x_0 + L). \tag{29}$$

From (29) it follows that for $(x_1, z_1) \in (x_0, x_0 + L/2] \times [A_0 + 2\varepsilon, A_1 - 2\varepsilon]$ there exists $z_0 \in [z_1 + \varepsilon, z_1 - \varepsilon]$ and $T \in (0, t_0)$ such that $x_\phi(T) = x_1$ and $z_\phi(T) = z_1$. The same proof works for $x_1 \in (x_0 - L/2, x_0]$.

*Step* 6: Let $E = \mathbb{R}^2$ when $r \in (0,1)$ or $a_2 \geqslant 0$ and $E = E(M_0)$ when $r \geqslant 1$ and $a_2 < 0$. Then from Steps 2–5 it follows that for any two points $(x_0, y_0) \in E$ and $(x, y) \in E$ there exist a control function $\phi$ and $T > 0$ such that $x_\phi(0) = x_0$, $y_\phi(0) = y_0$, $x_\phi(T) = x$ and $y_\phi(T) = y$. From Step 1 it follows that $k(T, x, y; x_0, y_0) > 0$ if $y \neq x + C$. $\square$

**Lemma 3.** *Assume that $\sigma \leqslant \rho$, $\beta\rho < \nu\sigma$ and let $E = E(M_0)$. Then for every density $f$ we have*

$$\lim_{t\to\infty} \iint_E P(t)f(x,y)\,\mathrm{d}x\,\mathrm{d}y = 1. \tag{30}$$

**Proof.** Similar to the proof of Lemma 2 we substitute $\zeta_t = \eta_t - \rho\sigma^{-1}\xi_t$. Then system (4), (5) can be replaced by

$$\mathrm{d}\xi_t = \sigma\,\mathrm{d}W_t + g_1(\xi_t,\zeta_t)\,\mathrm{d}t, \tag{31}$$

$$\mathrm{d}\zeta_t = g_2(\xi_t,\zeta_t)\,\mathrm{d}t \tag{32}$$

and the functions $g_1$ and $g_2$ are defined in (27). Since for each $\varepsilon > 0$ we have

$$\sup\{g_2(x,z)\colon z \geqslant M_0 + \varepsilon,\ x \in \mathbb{R}\} < 0, \tag{33}$$

we obtain $\limsup_{t\to\infty} \zeta_t \leqslant M_0$. We check that for almost every $\omega$ there exists $t_0 = t_0(\omega)$ such that $\zeta_t(\omega) < M_0$ for $t \geqslant t_0$. The case $\sigma = \rho$ is simple because $g_2(x,M_0) = -a_3 < 0$ for all $x \in \mathbb{R}$. Consider the case $\sigma < \rho$. If $\sigma < \rho$ then there exists $C_0 \in \mathbb{R}$ such that $g_2(C_0,M_0) = 0$. Fix $\kappa > 0$ and $\tau > 0$. Consider the solution $(\xi_t,\zeta_t)$ of system (31), (32) such that $\xi_0 = C_0 + 2\kappa$, $\zeta_0 = M_0 + \tau$. Let

$$A_{\kappa,\tau} = [C_0, C_0 + \kappa] \times [M_0, M_0 + \tau], \qquad B_{\kappa,\tau} = [C_0, C_0 + 2\kappa] \times [M_0, M_0 + \tau].$$

Then there exist $\varepsilon > 0$, $L > 0$ such that $g_2(x,z) < -\varepsilon$ for $x \geqslant C_0 + \kappa$, $z \in [M_0, M_0+\tau]$ and $|g_1(x,z)| \leqslant L$ for $(x,z) \in B_{\kappa,\tau}$. Let $\bar{\xi}_t$ be a solution of the equation $\mathrm{d}\bar{\xi}_t = \sigma\,\mathrm{d}W_t - L\,\mathrm{d}t$ with the initial condition $\bar{\xi}_0 = C_0 + 2\kappa$. Then $\bar{\xi}_t \leqslant \xi_t$ and $\zeta_t < M_0 + \tau - \varepsilon t$ as long as $(\xi_t,\zeta_t) \in B_{\kappa,\tau} \setminus A_{\kappa,\tau}$. Let $t = \tau/\varepsilon$ and $\Omega_\tau = \{\omega\colon\ \bar{\xi}_s(\omega) \geqslant C_0 + \kappa\colon\ \text{for } s \leqslant t\}$. Then $\lim_{\tau\to 0} \mathrm{Prob}(\Omega_\tau) = 1$ and $\zeta_t(\omega) < 0$ for $\omega \in \Omega_\tau$. Now let $(\xi_t,\zeta_t)$ be any solution of system (31), (32). Then from what has already been proved and from the Markov property it follows that if $\inf_{t>0} \zeta_t(\omega) \geqslant M_0$ then $\limsup_{t\to\infty} \xi_t(\omega) \leqslant C_0$. Analogously, we check that if $\inf_{t>0} \zeta_t(\omega) \geqslant M_0$ then $\liminf_{t\to\infty} \xi_t(\omega) \geqslant C_0$. Thus if $\inf_{t>0} \zeta_t(\omega) \geqslant M_0$ then $\lim_{t\to\infty} \xi_t(\omega) = C_0$. Assume that $\lim_{t\to\infty} \xi_t(\omega) = C_0$ with probability $> p_0 > 0$. Set $\gamma = g_1(C_0,M_0)$. Then for every $\varepsilon > 0$ there exist $t_0 > 0$ and a set $\Omega'$ such that $\mathrm{Prob}(\Omega') > p_0$, $|\xi_t(\omega) - C_0| < \varepsilon$ and

$$\sigma\,\mathrm{d}W_t + (\gamma - \varepsilon)\,\mathrm{d}t \leqslant \mathrm{d}\xi_t \leqslant \sigma\,\mathrm{d}W_t + (\gamma + \varepsilon)\,\mathrm{d}t \tag{34}$$

for $\omega \in \Omega'$ and $t \geqslant t_0$. Then $\mathrm{Prob}(\{\omega \in \Omega'\colon |\xi_{t_0+1} - C_0| < \varepsilon\}) \leqslant O(\varepsilon)$, which contradicts our assumption that $p_0 > 0$. Consequently, for almost every $\omega$ there exists $t_0 = t_0(\omega)$ such that $\zeta_t(\omega) < M_0$ for $t \geqslant t_0$ and (30) holds. □

**Lemma 4.** *The semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable or is sweeping with respect to compact sets.*

**Proof.** From Lemma 1 it follows that $\{P(t)\}_{t\geqslant 0}$ is an integral Markov semigroup with a continuous kernel $k(t,x,y)$ for $t > 0$. Let $E = \mathbb{R}^2$ when $\sigma > \rho$ or $\beta\rho \geqslant \nu\sigma$, and

$E = \operatorname{cl} E(M_0)$ when $\sigma \leqslant \rho$ and $\beta\rho < \nu\sigma$. Then according to Lemma 2 for every $f \in D$ we have

$$\int_0^\infty P(t)f \,\mathrm{d}t > 0 \quad \text{a.e. on } E. \tag{35}$$

If $\sigma > \rho$ or $\beta\rho \geqslant \nu\sigma$ then from Corollary 1 it follows immediately that the semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable or is sweeping with respect to compact sets. If $\sigma \leqslant \rho$ and $\beta\rho < \nu\sigma$ then for every density $f$ we have

$$\lim_{t\to\infty} \iint_E P(t)f(x,y)\,\mathrm{d}x\,\mathrm{d}y = 1. \tag{36}$$

This implies that it is sufficient to investigate the restriction of the semigroup $\{P(t)\}_{t\geqslant 0}$ to the space $L^1(E)$. From (35) the Foguel alternative also follows. □

**Lemma 5.** *If $c_1 > 0$ and $\mu c_2 < \delta c_1$ then the semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable.*

**Proof.** We will construct a nonnegative $C^2$-function $V$ and $R > 0$ such that

$$\sup_{\|x\|>R} \mathscr{A}^* V(x) < 0. \tag{37}$$

Such a function is called a Khasminskiĭ function. Using similar arguments to those in Pichór and Rudnicki (1997) one can check that the existence of a Khasminskiĭ function implies that the semigroup is not sweeping from the ball $\{x\colon \|x\| \leqslant R\}$. According to Lemma 4 the semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable, which will complete the proof. It remains to show that there exists a nonnegative $C^2$-function $V$ such that (37) holds. Recall that

$$\mathscr{A}^* V = \frac{1}{2}\sigma^2 \frac{\partial^2 V}{\partial x^2} + \sigma\rho \frac{\partial^2 V}{\partial x \partial y} + \frac{1}{2}\rho^2 \frac{\partial^2 V}{\partial y^2} + f_1 \frac{\partial V}{\partial x} + f_2 \frac{\partial V}{\partial y}. \tag{38}$$

Instead of writing a formula for $V$ we graphically explain how to construct $V$. The function $V$ is constant on the curves $\Gamma$ and $\Gamma'$ (see Fig. 1). For sufficiently large $x^2 + y^2$ the curves $\Gamma$ and $\Gamma'$ are constructed from line segments and from segments of circles with a constant and sufficiently large radius $r$. The distance $d$ between the parallel segments of $\Gamma$ and $\Gamma'$ is constant and $V(x_1, y_1) - V(x, y) = d$ for $(x, y) \in \Gamma$ and $(x_1, y_1) \in \Gamma'$. Fig. 2 shows the graphs of $\Gamma$ and $\Gamma'$ near a "vertice". For sufficiently large $x^2 + y^2$, the vectors $[f_1(x, y), f_2(x, y)]$ are directed inside the domains bounded by the curves $\Gamma$ and $\Gamma'$. Let

$$\mathscr{A}_1^* V = f_1 \frac{\partial V}{\partial x} + f_2 \frac{\partial V}{\partial y}, \tag{39}$$

$$\mathscr{A}_2^* V = \frac{1}{2}\sigma^2 \frac{\partial^2 V}{\partial x^2} + \sigma\rho \frac{\partial^2 V}{\partial x \partial y} + \frac{1}{2}\rho^2 \frac{\partial^2 V}{\partial y^2}. \tag{40}$$

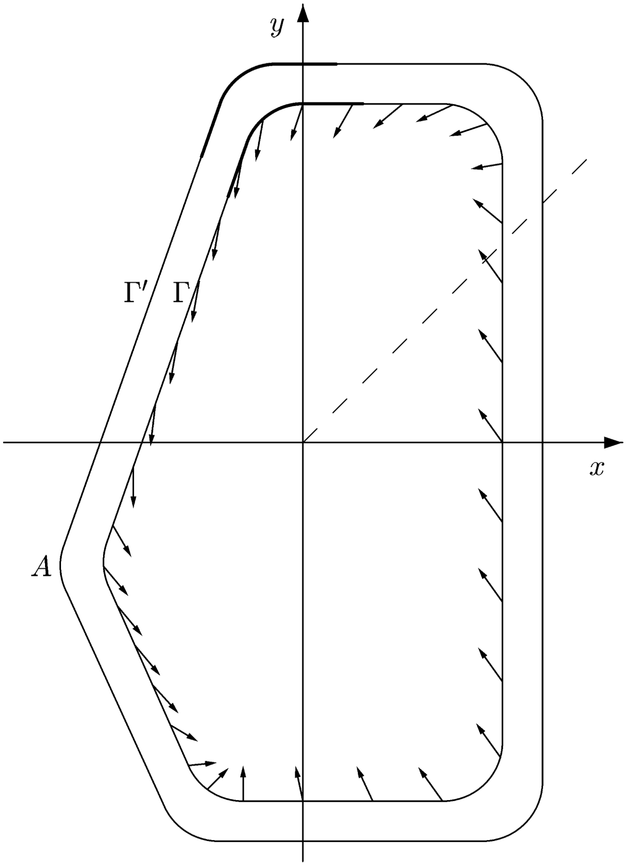


Fig. 1.

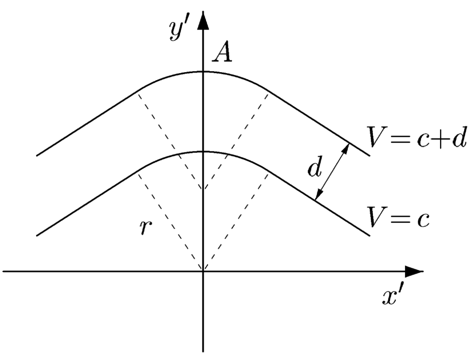


Fig. 2.

Then there exist constants $C_0 > 0$ and $R_0 > 0$ such that $\mathscr{A}_1^* V(x, y) \leqslant -C_0$ for $(x, y)$ such that $x^2 + y^2 > R_0^2$. We have $\mathscr{A}_2^* V(x, y) = O(1/r)$ for points from segments of circles of $\Gamma$ and $\mathscr{A}_2^* V(x, y) = 0$ for other points. Since $r$ can be chosen sufficiently large, there exists $R > R_0$ such that $\mathscr{A}_2^* V(x, y) \leqslant C_0/2$ when $x^2 + y^2 > R^2$. Consequently,

$$\mathscr{A}^* V(x, y) = \mathscr{A}_1^* V(x, y) + \mathscr{A}_2^* V(x, y) \leqslant -C_0/2$$

for $x^2 + y^2 > R^2$. □

In the proof of parts (II) and (III) of Theorem 1 we will use the following property of the solutions of a one-dimensional stochastic equation. Consider the following stochastic equation:

$$\mathrm{d}X_t = \sigma(X_t)\,\mathrm{d}W_t + b(X_t)\,\mathrm{d}t.$$

Let

$$s(x) = \int_0^x \exp\left\{-\int_0^y \frac{2b(r)}{\sigma^2(r)}\,\mathrm{d}r\right\}\mathrm{d}y.$$

If $s(-\infty) > -\infty$ and $s(\infty) = \infty$ then $\lim_{t\to\infty} X_t = -\infty$.

**Lemma 6.** *If* $c_1 < 0$ *then* $\lim_{t\to\infty} \xi_t = -\infty$ *and* $\lim_{t\to\infty} \eta_t = -\infty$.

**Proof.** If $c_1 < 0$ then

$$\mathrm{d}\xi_t \leqslant \sigma\,\mathrm{d}W_t + c_1\,\mathrm{d}t \tag{41}$$

and $\lim_{t\to\infty} \xi_t = -\infty$. Since $\lim_{t\to\infty} \xi_t = -\infty$ we have

$$\mathrm{d}\eta_t \leqslant \rho\,\mathrm{d}W_t - \frac{c_2}{2}\,\mathrm{d}t. \tag{42}$$

Since $c_2 = \gamma + \rho^2/2 > 0$, from (42) it follows that $\lim_{t\to\infty} \eta_t = -\infty$. □

**Lemma 7.** *If* $c_1 > 0$ *and* $\mu c_2 > \delta c_1$ *then* $\lim_{t\to\infty} \eta_t = -\infty$ *a.e. and the distribution of the process* $\xi_t$ *converges weakly to the measure which has the density* $f_*(x) = C\exp(2c_1 x/\sigma^2 - (2\mu/\sigma^2)\mathrm{e}^x)$.

**Proof.** Consider the following equation:

$$\mathrm{d}\bar{\xi}_t = \sigma\,\mathrm{d}W_t + (c_1 - \mu\mathrm{e}^{\bar{\xi}_t})\,\mathrm{d}t. \tag{43}$$

If $\xi_0 = \bar{\xi}_0$ then $\xi_t \leqslant \bar{\xi}_t$. This implies that $\eta_t$ satisfies the inequality

$$\mathrm{d}\eta_t \leqslant \rho\,\mathrm{d}W_t + (-c_2 + \delta\mathrm{e}^{\bar{\xi}_t})\,\mathrm{d}t. \tag{44}$$

Then

$$\eta_t \leqslant \eta_0 + \rho W_t - c_2 t + \int_0^t \delta\mathrm{e}^{\bar{\xi}_s}\,\mathrm{d}s. \tag{45}$$

Eq. (43) has a stationary solution which has the density $f_*(x) = C\exp(2c_1x/\sigma^2 - (2\mu/\sigma^2)\mathrm{e}^x)$, where $C$ is some constant. From the ergodic theorem it follows that

$$\lim_{t\to\infty}\frac{1}{t}\int_0^t \mathrm{e}^{\bar{\xi}_s}\,\mathrm{d}s = \int_{-\infty}^{\infty}\mathrm{e}^x f_*(x)\,\mathrm{d}x \quad \text{a.e.} \tag{46}$$

Since $f'_*(x) = (2c_1/\sigma^2 - (2\mu/\sigma^2)\mathrm{e}^x)f_*(x)$ we have

$$\int_{-\infty}^{\infty}\mathrm{e}^x f_*(x)\,\mathrm{d}x = \int_{-\infty}^{\infty}\frac{c_1}{\mu}f_*(x)\,\mathrm{d}x = \frac{c_1}{\mu}. \tag{47}$$

From (46), (47) we obtain

$$\lim_{t\to\infty}\frac{1}{t}\int_0^t \delta\mathrm{e}^{\bar{\xi}_s}\,\mathrm{d}s = \frac{c_1\delta}{\mu}. \tag{48}$$

Since $\lim_{t\to\infty}\frac{1}{t}\rho W_t = 0$ from (44) and (48) it follows that

$$\limsup_{t\to\infty}\frac{\eta_t}{t} \leqslant \frac{c_1\delta}{\mu} - c_2 < 0.$$

Consequently $\lim_{t\to\infty}\eta_t = -\infty$. Thus for arbitrary small $\varepsilon > 0$ there exist $t_0$ and a set $\Omega_\varepsilon$ such that $\mathrm{Prob}(\Omega_\varepsilon) > 1-\varepsilon$ and $\beta\mathrm{e}^{\eta_t(\omega)} \leqslant \varepsilon$ for $t \geqslant t_0$ and $\omega\in\Omega_\varepsilon$. Now from the inequalities

$$\sigma\,\mathrm{d}W_t + (c_1 - \varepsilon - \mu\mathrm{e}^{\xi_t})\,\mathrm{d}t \leqslant \mathrm{d}\xi_t \leqslant \sigma\,\mathrm{d}W_t + (c_1 - \mu\mathrm{e}^{\xi_t})\,\mathrm{d}t \tag{49}$$

it follows that the distribution of the process $\xi_t$ converges to the measure with the density $f_*$. □

**Remark 4.** One can consider the Lotka–Volterra system (3) with different kinds of stochastic perturbations. For example if we replace the terms $\sigma X_t\,\mathrm{d}W_t$ and $\rho Y_t\,\mathrm{d}W_t$ in (1), (2) by terms $\sigma X_t\,\mathrm{d}W_t^1$ and $\rho Y_t\,\mathrm{d}W_t^2$ where $W_t^1$, $W_t^2$ are independent Wiener processes then the corresponding system (4), (5) is easier to analyse because it generates an integral Markov semigroup with a continuous and strictly positive kernel. According to Corollary 1 this semigroup is asymptotically stable or is sweeping with respect to compact sets. In this case Theorem 1 still holds. Generally, if we have non-degenerate diffusion then the existence of a Khasminskiĭ function implies asymptotic stability. Arnold et al. (1979) considered a model where only the prey population is stochastically perturbed, i.e. the model described by system (1), (2) with $\rho = 0$. Also in this case Theorem 1 holds. A special role in applications is played by the Lotka–Volterra system with $\mu=\nu=0$. One can check that in this case the semigroup satisfies the Foguel alternative. Since in this case we do not have a stationary distribution, the semigroup is sweeping with respect to compact sets. A precise analysis of the Lotka–Volterra system with $\mu=\nu=0$ is given in the paper by Khasminskiĭ and Klebaner (2001).

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## References

Aida, S., Kusuoka, S., Strook, D., 1993. On the support of Wiener functionals. In: Elworthy, K.D., Ikeda, N. (Eds.), Asymptotic Problems in Probability Theory: Wiener Functionals and Asymptotic. Pitman Research Notes in Mathematical Series, Vol. 284, Longman Scient. Tech., pp. 3–34.

Arnold, L., Horsthemke, W., Stucki, J.W., 1979. The influence of external real and white noise on the Lotka–Volterra model. Biomedical J. 21, 451–471.

Ben Arous, G., Léandre, R., 1991. Décroissance exponentielle du noyau de la chaleur sur la diagonale (II). Probab. Theory Related Fields 90, 377–402.

Chessa, S., Fujita Yashima, H., 2002. The stochastic equation of predator–prey population dynamics (Italian). Boll. Unione Mat. Ital. Sez. B Artic. Ric. Mat. 5 (8), 789–804.

Foguel, S.R., 1979. Harris operators. Israel J. Math. 33, 281–309.

Khasminskiĭ, R.Z., Klebaner, F.C., 2001. Long term behaviour of solutions of the Lotka–Volterra system under small random perturbations. Ann. Appl. Probab. 11, 953–963.

Komorowski, T., Tyrcha, J., 1989. Asymptotic properties of some Markov operators. Bull. Polish Acad. Sci. Math. 37, 221–228.

Lasota, A., Mackey, M.C., 1994. Chaos, fractals and noise. Stochastic aspects of dynamics. In: Springer Applied Mathematical Sciences, Vol. 97. Springer, New York.

Malliavin, P., 1978a. Stochastic calculus of variations and hypoelliptic operators. In: Itô, K. (Ed.), Proceedings of the International Symposium on Stochastic Differential Equations of Kyoto 1976. Wiley, New York, pp. 195–263.

Malliavin, P., 1978b. $C^k$-hypoellipticity with degeneracy. In: Friedman, A., Pinsky, M. (Eds.), Stochastic Analysis. Academic Press, New York, pp. 199–214.

Norris, J., 1986. Simplified Malliavin calculus. In: Séminaire de probabilitiés XX, Lecture Notes in Mathematics, Vol. 1204. Springer, New York, pp. 101–130.

Pichór, K., Rudnicki, R., 1997. Stability of Markov semigroups and applications to parabolic systems. J. Math. Anal. Appl. 215, 56–74.

Pichór, K., Rudnicki, R., 2000. Continuous Markov semigroups and stability of transport equations. J. Math. Anal. Appl. 249, 668–685.

Rudnicki, R., 1995. On asymptotic stability and sweeping for Markov operators. Bull. Polish Acad.: Math. 43, 245–262.

Rudnicki, R., Pichór, K., Tyran-Kamińska, M., 2002. Markov semigroups and their applications, Markov semigroups and their applications. In: Garbaczewski, P., Olkiewicz, R. (Eds.), Dynamics of Dissipation. Lecture Notes in Physics, Vol. 597. Springer, Berlin, pp. 215–238.

Stroock, D.W., Varadhan, S.R.S., 1972. On the support of diffusion processes with applications to the strong maximum principle. Proceedings of the Sixth Berkeley Symposium on Mathematical Statistics and Probability, Vol. III. Univ. Cal. Press, Berkeley, pp. 333–360.

Volterra, V., 1931. Leçons sur la théorie mathematique de la lutte pour la vie. Gauthier-Villar, Paris.